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BULLETIN OF
MATHEMATICAL BIOPHYSICS
VOLUME 9, 1947

AN APPROACH TO A NEUROBIOPHYSICAL INTERPRETATION OF MOTIVATIONAL INTERACTIONS

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Some problems of the interaction between two individuals are considered in terms of the theory of neural nets. Among these are: the effect of individual differences on the total output of two individuals who share equally the results of their effort; the problem of stability of the equilibrium effort; the problem of the division of the results of a cooperative effort, and the effect of individual differences in the parameters on the results; the case in which two types of activity are possible—one cooperative, the other solitary; and the effect of certain parameters on the fraction of effort spent in each kind of activity.

A number of problems involving the interaction between individuals have been considered in terms of maximizing a satisfaction function (Rashevsky, 1947; Rapoport, 1947). It is the purpose here to consider such problems in terms of the activity of neural nets which are able to influence each other. The relation between this approach and that referred to above will be discussed subsequently.

We shall consider first a representation of the case in which an individual in response to a given situation works to produce goods of value to himself.

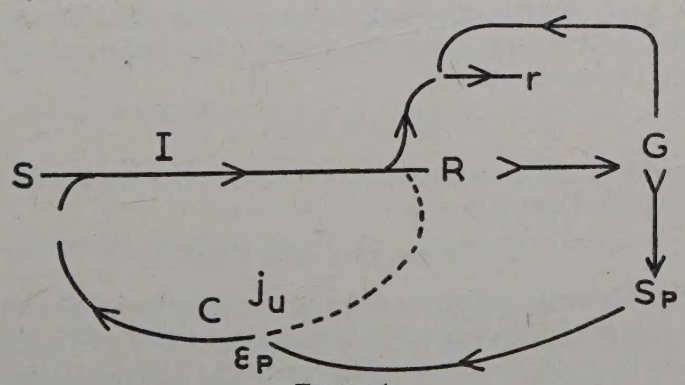

FIGURE 1

Consider first the neural net (Figure 1) which is taken to represent the individual in this situation. Let a stimulus S be capable of initiating some response R through a nerve pathway I having a collateral which stimulates an inhibitory pathway leading to a center C. Let the response R, which may be referred to as an effort, lead to the

production of some quantity (e.g., goods) which is itself potentially a stimulus or leads to a stimulus, S_p, which acts upon a nerve pathway leading to the center C. From C another pathway connects with I. For the present we shall not consider the response r indicated in the Figure. Causal relations not within the net are indicated by double-headed arrows.

We shall make the following simplifying assumptions about the pathways represented in the Figure (Rashevsky, 1938, 1945). In the stationary state, let the excitation ε_p at the center C be given by

$$\varepsilon_p = k \log (1 + \alpha' S_p) , \tag{1}$$

where α' and k are constants. In this case the stimulus S_p is considered to be equivalent to G; and, for this case only, let the amount of goods produced be proportional to R, so that

$$\alpha' S_p = \alpha' G = \alpha R . \tag{2}$$

Let the inhibition j_u at the center C be proportional to the degree of response R, which is taken to be proportional to the excitation ε_R at the efferent connections of the pathway I. Thus, if β is a constant,

$$j_u = \beta R . \tag{3}$$

Define σ as the net excitation at C given by

$$\sigma = \varepsilon_p - j_u + \sigma_0 , \tag{4}$$

where σ_0 is the contribution from other sources not indicated in the Figure. We shall neglect σ_0 for the present. If γ and γ' are constants, then R will be approximately

$$R = \gamma' S + \gamma \sigma . \tag{5}$$

For convenience, we shall neglect the $\gamma' S$, considering S only as starting the process. Then if $\gamma' = \sigma_0 = 0$, we have

$$R = \gamma k \log (1 + \alpha R) - \gamma \beta R \tag{6}$$

as the equation from which to determine the value of R. Only positive, real values of R have physical meaning, so that $\gamma k \alpha > \beta \gamma + 1$.

Denote by $\bar{R}$ and $\bar{\sigma}$ the solutions for R and σ in equations (6) and (5). If we consider σ to be a measure of satisfaction and R a measure of the effort, then $\bar{R}$ is the steady-state or equilibrium effort and $\bar{\sigma}$ is the equilibrium value of the satisfaction. If we assume that the time constant, $1/a$, for the pathway I is very small compared with any other time delay (e.g., the time involved between R and S_p), then it can be seen that the equilibrium is stable, any change in $\bar{R}$ or $\bar{\sigma}$ spon-

taneously resulting in changes leading to a return to the equilibrium value.

Suppose that two different individuals act according to the above equations, each acting independently. Let $R_{1s} + R_{2s}$ be the total effort of the two individuals, the total amount of goods produced being proportional to the total effort in this case. We may now ask what happens to the total effort $R_{1c} + R_{2c}$ when the total amount of goods produced by both is shared equally between them. We shall consider only the case in which the two individuals differ only slightly in their parameters. Thus, for example, if $\bar{\alpha}$ is the average value of the parameters α_1 and α_2 for the two individuals, and if δ_2 is a fraction measuring the relative deviation of either from the average, then $\alpha_1 = \bar{\alpha}(1 + \delta_2)$ and $\alpha_2 = \bar{\alpha}(1 - \delta_2)$. Let δ_1 and δ_3 be similar small deviations. Then instead of equation (6) we may write

$$R_{1c} = \bar{\gamma}\bar{k}(1 + \delta_1) \log (1 + \bar{\alpha} + \bar{\alpha}\delta_2 R_{1c}) - \bar{\gamma}\bar{\beta}(1 + \delta_3) R_{1c}, \tag{7}$$

with a similar expression for R_{2c} in which each of the δ's is of opposite sign. If the two now work separately, one can solve for the total effort $R_{1s} + R_{2s}$, retaining only first and second degree terms in the δ's. If, instead, they work together sharing equally, the $\alpha's_p$ being equal to $\alpha(R_{1c} + R_{2c})/2$, their total effort can be determined to be some quantity $R_{1c} + R_{2c}$. The difference $R_{1c} + R_{2c} - (R_{1s} + R_{2s})$ can be determined and is found to depend upon δ_1, δ_2, and δ_3 in such a way that equal sharing of the goods produced—

a) decreases the total effort if $\delta_1 \neq 0$, $\delta_2 = \delta_3 = 0$;

b) increases the total effort if $\delta_1 = \delta_3 = 0$, $\delta_2 \neq 0$;

c) decreases the total effort if $\delta_1 = \delta_2 = 0$, $\delta_3 \neq 0$.

We consider next a case in which the division of G is not imposed from without, but is determined by the individuals themselves. Let a response r, initiated by G which acts as a stimulus and is augmented by a collateral from pathway I, be a response which results in an effort by the individual to acquire and retain as much as possible of G. Introduce also the possibility that the total amount of goods produced in a cooperative effort may be greater than the sum of the two amounts produced separately. Thus let

$$G_T = G_1 + G_2 + 2\theta G_1 G_2, \tag{8}$$

where θ is a measure of the efficiency of the cooperation. Now let G_T be divided in proportion to the strength of the responses r so that if F_1 is the fraction obtained by the first individual, and if r is of the form $sG_T + mR$, s and m being constants, then

$$F_1 = \frac{r_1}{r_1 + r_2} = \frac{s_1 G_T + m_1 R_1}{(s_1 + s_2) G_T + m_1 R_1 + m_2 R_2}. \tag{9}$$

We shall now give the results for several cases. In all cases it is assumed that $G_T = R_1 + R_2 + 2\theta R_1 R_2$, $S_p = FG_T$, $\alpha = \alpha'$, $k_1 = k_2 = 1$, $a_1 = a_2 = 1$, $\alpha_1 = \alpha_2 = 6.42$, $s_1 + s_2 = 2s$, $\beta_1 + \beta_2 = 0.2$. Then the effort $\bar{R}$ of a single average individual with $\beta = 0.1$ is 9. The reasons for choosing certain of the numerical values for the constants will be discussed subsequently. The quantities η, ζ, and ν, used below, are measures of deviation from the average values of the parameters.

Case 1. If $m_1 = m_2 >> s$, $\beta_1 = (1 - \eta)/10$, $\beta_2 = (1 + \eta)/10$ $(\eta \geqq 0)$, then on expanding we find:

$$R_1 = \bar{R} + 5.8\eta + 2.6\eta^2 + 52\theta + \cdots,$$

$$R_2 = \bar{R} - 5.8\eta + 2.6\eta^2 + 52\theta + \cdots,$$

so that $G_1/G_2 = R_1/R_2 = 1 + 1.28\eta + \cdots$, $R_1 + R_2 = 2\bar{R} + 5.3\eta^2 + 104\theta + \cdots$, $G_1 + G_2 = 2\bar{R} + 5.3\eta^2 + 266\theta + \cdots$, but $R_{1s} = R_1$ and $R_{2s} = R_2$. Thus, if $\theta = 0$, the result is the same as if there had been no cooperation.

Case 2. If $m_1 = m_2 << s$, $s_1 = s_2$, $\beta_1 = (1 - \eta)/10$, $\beta_2 = (1 + \eta)/10$, then

$$R_1 = \bar{R} + 3.5\eta + 52\theta + 2.3\eta^2 + \cdots,$$

$$R_2 = \bar{R} - 3.5\eta + 52\theta + 2.3\eta^2 + \cdots,$$

so that $G_1/G_2 = 1$, $R_1/R_2 = 1 + 0.8\eta + \cdots$, $R_1 + R_2 = 2\bar{R} + 4.5\eta^2 + 104\theta + \cdots = R_{1s} + R_{2s} - 0.8\eta^2 + 104\theta$, $G_1 + G_2 = 2\bar{R} + 4.5\eta^2 + 266\theta + \cdots$. Thus, for $\theta = 0$, the total output is less than under the conditions of solitary effort, but the ratio of the efforts is somewhat closer to one. If $\theta \geqq 0.008\eta^2$, the total effort is greater than $R_{1s} + R_{2s}$, while θ need be greater than only $0.003\eta^2$ for the total cooperative output to be greater than the combined solitary outputs.

Case 3. If $\beta_1 = \beta_2$, $m_1 = \bar{m}(1 + \zeta) >> s$, then

$$R_1 = \bar{R} + 5.8\zeta + 52\theta - 7\zeta^2 + \cdots,$$

$$R_2 = \bar{R} - 5.8\zeta + 52\theta - 7\zeta^2 + \cdots,$$

so that $G_1/G_2 = 1.33\zeta + \cdots$, $R_1/R_2 = 1 + 1.28\zeta + \cdots$, $R_1 + R_2 = 2\bar{R} - 14\zeta^2 + 104\theta + \cdots$, $G_1 + G_2 = 2\bar{R} - 14\zeta^2 + 266\theta$, $\bar{R} = R_{1s} = R_{2s}$. In this case, where the amount of effort determines the division of G, the total effort is reduced if the coefficients m_1 and m_2 are unequal and if $\theta = 0$. The individual with the largest m exerts more effort and receives a proportionately larger share. If $\theta > 0.026\zeta^2$, the output G will be increased but effort will not be increased unless $\theta > 0.07\zeta^2$.

Case 4. If $\beta_1 = \beta_2$, $m_1 = m_2 << s$, $s_1 = s(1 + \nu)$, $s_2 = s(1 - \nu)$, then

$$R_1 = \bar{R} + 3.5\nu + 52\theta - 2.6\nu^2,$$
$$R_2 = \bar{R} - 3.5\nu + 52\theta - 2.6\nu^2,$$

so that $G_1/G_2 = 1 + 2\nu + \cdots$, $R_1/R_2 = 1 + 0.8\nu + \cdots$, $R_1 + R_2 = 2\bar{R} - 5.2\nu^2 + 104\theta + \cdots$, $G_1 + G_2 = 2\bar{R} - 5.2\nu^2 + 266\theta$, $R = R_{1s} = R_{2s}$. This case, in which the division is independent of the efforts, gives substantially the same results as the case in which the division is proportional to the efforts, except that the individual exerting the most effort receives a relatively larger share.

In none of these cases have we considered the effect of disproportionate sharing as it acts as a stimulus to influence the response of the individuals. If the stimulus is in proportion to the excess of the quantity G_1 going to one individual over G_2 going to the other, then to a first approximation the result is the same whether the excess acts as a stimulus to pathways leading to C or to the pathway beginning at S_p. If ϕ^- is a coefficient measuring the decrease in the net excitation at C for either individual due to the other individual receiving a larger share, while ϕ^+ is a corresponding coefficient measuring the increase in the net excitation due to that individual receiving a greater share, then the total effort will be decreased unless $\phi^+ > \phi^-$. On the other hand, the ratio R_1/R_2 is increased in each of the above cases.

The above results indicate some of the possible effects of individual differences on the interaction under the special assumptions made. Somewhat more general results can be expected if the assumption of particular numerical values for the constants is removed.

Thus far we have considered only one possible action open to each individual. We shall consider next a case in which there are two possible reactions; for simplicity, we assume no bias in favor of either. We shall consider that one response R_s is that of a solitary effort resulting in some quantity G_s which is retained by that individual. The other response R_c is a cooperative effort resulting in G_c.

We consider these to be more or less independent responses, but each interferes with the other to some extent. For this case, for simplicity, we shall consider the individuals to be identical so that the goods G_c, produced in cooperation, are always equally divided.

This situation may be represented by the following neural mechanism. Let each individual be represented by two mechanisms indicated in Figure 1, with the following additions. Pathways leading to the response r may be omitted from consideration in this case since the results of cooperative effort are equally divided, the individuals being identical. The subscripts s and c will be used to label parts of the two neural nets. Let an inhibitory pathway, acted upon by I_s, lead to the center C_c, producing an amount of inhibition lR_s, the parameter l being a constant for this pathway. From symmetry, II_c and C_s will be similarly connected, the amount of inhibition at C_s being lR_c. We shall assume, as in equation (7), that the cooperative effort may be more efficient than the solitary effort. Furthermore, suppose that the amount G_{1c} which one individual obtains due to his cooperative effort acts as a stimulus to the other individual which results in an inhibitory state at the center C_{2c} (the subscripts 1 and 2 referring to the individuals) of magnitude $\delta' G_{2c}$, where δ' is a constant. Since the individuals are assumed identical, we may drop the subscripts 1 and 2.

We may now write the differential equation for the excitatory states at the efferent ends of the pathways I_s and I_c. Since these are proportional to R_s and R_c, the proportionality constant being some quantity a'/a, we may then write

$$\frac{dR_c}{dt} = a'g\left[k\log\left(1 + \alpha R_c + \frac{\alpha^2}{\alpha'}\theta R_c^2\right) - \beta R_c - lR_s - \delta R_c\right] - aR_c, \tag{10}$$

where g is a parameter of the pathway connecting C_s and I_s and $\delta = \alpha\delta'/\alpha'$. A similar expression for R_s may be obtained by interchanging subscripts and setting $\delta = \theta = 0$. Setting $dR_c/dt = 0$ and solving R_s in terms of R_c, we have from equation (10)

$$R_s = \frac{1}{l}\left[a'gk\log\left(1 + \alpha R_c + \frac{\alpha^2\theta}{\alpha'}R_c^2\right) - a'g\beta R_c - a'\delta g R_c - aR_c\right] \tag{11}$$

for the equation of a line (curve A, Figure 2) separating regions for

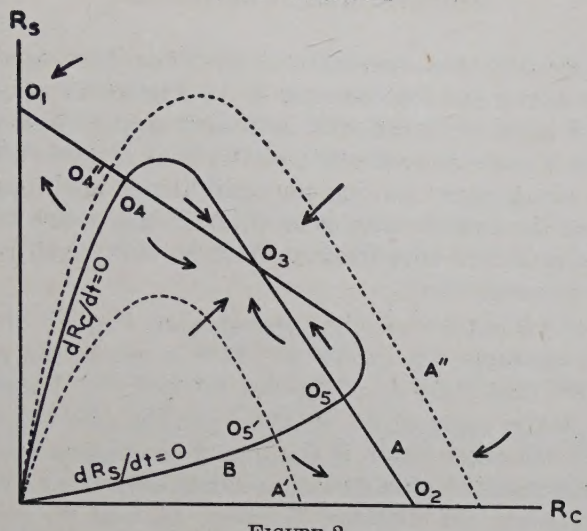

FIGURE 2

which dR_c/dt is positive from regions where it is negative. The corresponding line (curve B, Figure 2) for $dR_s/dt = 0$ is given by

$$R_c = \frac{1}{l}\,[a'gk \log\,(1 + \alpha R_s) - a'g\beta R_s - aR_s]\,. \tag{12}$$

First let $\delta = \theta = 0$, so that R_c is actually equivalent to R_s. Thus two equivalent activities are possible in this case. The results are shown graphically in Figure 2 for a special choice of the parameters. The dotted curves may be ignored for the present.

The coordinates of any point on the curve A labeled $dR_c/dt = 0$, when substituted into equation (10), make the right-hand side zero. Any point above it for which R_s is increased evidently makes the right-hand side, and therefore dR_c/dt, smaller $(-lR_s)$ and hence negative. Conversely, at any point below this curve, $dR_c/dt > 0$. Similarly, everywhere to the right of curve B, $dR_s/dt < 0$; and to the left of it $dR_s/dt > 0$. The arrows in the Figure indicate the direction toward which R_s and R_c tend to move. From this it can be seen that the points O_1, O_2, and O_3 are points of stable equilibrium, while O_4 and O_5 are unstable. The point O_3 represents a situation in which the effort is equally divided between the two types of activity R_s and R_c. If for some reason R_s is now very much reduced for a sufficiently long time, then a new stable equilibrium is reached in which $R_s = 0$ and R_c is given by the ordinate of point O_2. Similarly, if R_c is increased sufficiently, the system will move over to O_1, no effort being spent on the "cooperative" effort.

Next suppose that $\theta = 0$ but $\delta \neq 0$. Then, instead of curve A, one obtains a curve (as for example A' in Figure 2) which is below A. Thus if δ is small, there will be a new equilibrium position O_3' (not shown in Figure 2) to the left of O_3. For larger δ's this merges with O_4 and disappears, leaving no equilibrium positions except O_1 and O_2. Thus the system moves to O_1 with the result that for any larger values of δ, the cooperative effort R_c will be discontinued in favor of independent effort.

Now if $\delta = 0$ but $\theta \neq 0$, then one obtains, instead of A, a curve above A—for example, the curve A''. If θ is small, the new equilibrium point O_3'' (not shown) will move toward O_5, disappearing for a sufficiently large value of θ. In this case the effort is entirely cooperative. On the other hand, if the initial conditions were such that solitary efforts resulted, this situation would continue. For large values of θ, however, the distance between O_1 and O_4 may be small enough so that a small degree of accidental cooperation would be sufficient to result in a spontaneous change to complete cooperation.

We may inquire into the relation between the method of the present paper and the method of maximizing the satisfaction function. If it happens that $\gamma = R^*/\sigma^*$, where $R^* = k/\alpha\beta - 1/\alpha$ and $\sigma^* = k \log k/\beta - k/\alpha + \beta/\alpha$, then $\bar{\sigma}$, the solution for σ from equations (6) and (5), is equal to σ^*, which is also the maximum value of σ in the equation resulting from eliminating R from equations (5) and (6) ($\gamma' S = 0$). In this special case σ corresponds to a satisfaction function (Rashevsky, 1947). Actually γ need only have approximately the value specified, since the second derivative of σ with respect to R is zero at R^*. But if there is interaction between individuals having different parameters, the interpretation of σ as a satisfaction function, even if $\gamma = R^*/\sigma^*$, can no longer be made except as an approximation. The numerical values used in cases (1) to (4) were such that $\gamma = R^*/\sigma^*$, and thus correspond approximately to maximizing σ. One can see in these cases that the values of σ are not exactly at a maximum.

Somewhat more generally, if σ' is the excitation at some center which has collaterals coming from center C and pathway I, then σ' can be considered to be a satisfaction function if the parameter of the pathway from I has a particular value. This value can be readily determined. However, the quantity σ' is merely an indicator and serves no other function. Also, the quantity σ', in general, is not equivalent to a satisfaction function if one treats the case of the interaction of two or more individuals having different parameters. Furthermore, the addition of satisfaction over individuals has no

meaning in the present formulation although the corresponding problems can still be treated.

The author wishes to express his appreciation to Professor N. Rashevsky and to Dr. A. Rapoport for reading and discussing the manuscript.

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CONTRIBUTIONS TO THE THEORY OF ORGANIC FORM: THE INTESTINAL TRACT

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By making some assumptions concerning the symmetry of certain "classes" of vertebrates and other assumptions concerning the mode of absorption of food by the small intestine, an equation is developed which gives a relation between the length of the small intestine and the total mass of an animal. The equation contains parameters which depend upon the category of vertebrates (carnivorous, omnivorous, etc.) with which the animal is to be associated. The paper also contains a brief discussion of the parameters of the equation and some of the implications which stem from assumptions about their relative magnitudes. In particular, it is noted that the constant of proportionality in the equation which relates intestine length to a power of the body mass is found to be inversely proportional to the square of the "energy content" of the food which makes up the animal's diet. Some suggestions are offered which may lead to an experimental evaluation of the parameters.

This paper is concerned with the problem of correlating the geometry of the gastrointestinal tract of vertebrates—in particular the small intestine—with certain factors of nutrition.

Let it be assumed that of the animals to be considered, those with similar nutritive habits are geometrically similar. This assumption implies that any linear dimension of one of the animals is directly proportional to the cube root of any one of its volume dimensions. In particular, if L is the length of its small intestine, V the total volume of the animal, and C a constant of proportionality, we can write

$$L = CV^{1/3}. \tag{1}$$

If we now make the additional assumption that the volume of the animal is roughly proportional to its mass M, then by substituting the expression $V = C_2M$ in equation (1) and letting $C_1C_2^{1/3} = \lambda$, we obtain

$$L = \lambda M^{1/3}. \tag{2}$$

Thus equation (2), which follows from the two initial assumptions, states that the lengths of the small intestines of the series of animals, to be considered having the same nutritive habits, are proportional to the cube root of their total masses.

By making different (but comparable) assumptions, we will attempt in what follows to relate the constant of proportionality λ to certain other parameters which are associated with the dietary habits of the animals in question. We shall consider the following assumptions:

1. The small intestine is a right circular cylinder of length L and radius r.
2. A solution of a (food) substance A which is absorbable at the surface of the intestine has an "available" energy content of e_0 calories per gram.
3. The solution also contains a substance B which is not absorbable by the intestine, but in the process of digestion is converted to substance A.
4. The solution moves through the small intestine at a constant velocity u.
5. The rate of absorbtion of substance A at the surface of the small intestine is a function $f(c_a)$ of the average concentration c_a of A (gm/cm^3) in an infinitesimal orthogonal slice through the small intestine.
6. The rate of production of A from B is a function $g(c_b)$ of the average concentration c_b of B in an infinitesimal orthogonal slice through the small intestine.
7. The rate of "mechanical transfer" of A and B at the velocity u is sufficiently large to allow for neglecting the transport of those substances by diffusion.
8. The rate of metabolism of the animals in question is given by the expression

$$R = kM^p, \qquad (\tfrac{2}{3} \leqq p \leqq \tfrac{3}{4}),$$

in which R denotes the rate of metabolism, M the mass of the animal, and k a constant of proportionality.

The first problem to be considered is the rate of absorbtion of energy E at the surface of the small intestine. This rate is given by the expression

$$E = 2\pi r e_0 \int_0^L f(c_a)\,dx\,. \tag{3}$$

In order to evaluate the above integral it is necessary to express c_a as a function of x and also to know the form of the function f.

Hereafter, the following notation will be employed:

$t = x/u =$ the time taken by an infinitesimal orthogonal element of volume to travel from 0 to x.

$c_{0a} =$ the concentration of A at the point $x = 0$.

c_{0b} = the concentration of B at the point $x = 0$.

$A(t)$ = the concentration of A in an infinitesimal element of volume which has moved through the intestine for a time t.

$B(t)$ = the concentration of B in an infinitesimal element of volume which has moved through the intestine for a time t.

Using the above notation, we obtain

$$A(t) = c_{0a} + \int_0^t g[B(t)]dt - \int_0^t \frac{2}{r} f[A(t)]dt. \tag{4}$$

By substituting x/u for t, $(1/u)dx$ for dt, $\bar{c}_a(x/u)$ for $A(t)$, and $\bar{c}_b(x/u)$ for $B(t)$ in equation (4), we obtain

$$\begin{aligned} \bar{c}_a(x/u) = c_{0a} &+ \int_0^{x/u} g[\bar{c}_b(x/u)]d(x/u) \\ &- \int_0^{x/u} \frac{2}{r} f[\bar{c}_a(x/u)]d(x/u). \end{aligned} \tag{5}$$

By differentiation of equation (5), we obtain

$$\frac{d\bar{c}_a}{d(x/u)} = g[\bar{c}_b(x/u)] - \frac{2}{r} f[\bar{c}_a(x/u)]. \tag{6}$$

Now recalling that u is assumed to be a constant, we can consider the concentration of A to be a function $c_a(x)$ of x and the concentration of B to be a function $c_b(x)$ of x such that

$$\frac{dc_a(x)}{(1/u)\,dx} = g[c_b(x)] - \frac{2}{r} f[c_a(x)].$$

After rearranging the above expression, we obtain

$$c_a' = \frac{1}{u} g(c_b) - \frac{2}{ru} f(c_a). \tag{7}$$

By similar considerations, we obtain

$$c_b' = -\frac{1}{u} g(c_b). \tag{8}$$

In order to evaluate the integral in expression (3), it will be necessary to make some assumptions about the form of the functions $f(c_a)$ and $g(c_b)$. Several simple cases will be considered.

Case 1. Let $0 < f(c_a) = k_1$ and $0 < g(c_b) = k_2$, where k_1 and k_2 are constants.

By imposing the above conditions on equation (8), we obtain

$$c_b' = -\frac{k_2}{u}. \tag{9}$$

By integrating equation (9), we obtain

$$c_b = -\frac{k_2}{u}x + k_3, \tag{10}$$

where k_3 is a constant of integration. If we impose the boundary condition that $c_b = c_{0b}$ at $x = 0$, we obtain $c_{0b} = k_3$; hence the complete solution of equation (9) is

$$c_b = c_{0b} - \frac{k_2}{u}x. \tag{11}$$

Equation (7) can be written for this case:

$$c_a' = \frac{1}{u}k_2 - \frac{2}{ru}k_1. \tag{12}$$

By integrating equation (12) and imposing the boundry condition that $c_a = c_{0a}$ at $x = 0$, we obtain

$$c_a = c_{0a} + \left(\frac{k_2}{u} - \frac{2k_1}{ru}\right)x. \tag{13}$$

Introducing the conditions of Case 1 into equation (3), we obtain

$$E = 2\pi r e_0 \int_0^L k_1 dx,$$

or

$$E = 2\pi r e_0 k_1 L. \tag{14}$$

The equations are somewhat more complicated if the breakdown of the unabsorbable solute is assumed to proceed at a rate given by the expression $g(c_b) = k_2 c_b$.

Case 2. Let $0 < f(c_a) = k_1$ and $0 < g(c_b) = k_2 c_b$, where k_1 and k_2 are constants.

For Case 2, equation (8) becomes

$$c_b' = -\frac{k_2}{u}c_b. \tag{15}$$

By integrating equation (15) and imposing the boundry conditions, we obtain

$$c_b = c_{0b} e^{-\frac{k_2}{u} x} . \tag{16}$$

Similarly, the expression derived for c_a under the conditions of Case 2 is

$$c_a = c_{0a} + c_{0b} \left(1 - e^{-\frac{k_2}{u} x}\right) - \frac{2k_1}{ru} x. \tag{17}$$

The value of E as given by expression (3) is, as before, $E = 2\pi k_1 erL$.

Case 3. Let $0 < f(c_a) = k_1 c_a$ and $0 < g(c_b) = k_2$, where k_1 and k_2 are constants.

For Case 3, equation (8) becomes

$$c_b' = -\frac{k_2}{u}. \tag{18}$$

After integrating equation (18) and imposing boundry conditions, we obtain for Case 3:

$$c_b = c_{0b} - \frac{k_2}{u} x. \tag{19}$$

By similar considerations we find for Case 3:

$$c_a = \left(c_{0a} - \frac{rk_2}{2k_1}\right) e^{-\frac{2k_1}{ru} x} + \frac{rk_2}{2k_1}. \tag{20}$$

By evaluating the integral of expression (3) for this case, we obtain

$$E = 2\pi r e_0 k_1 \left[\frac{rk_2}{2k_1} L + \frac{ru}{2k_1} \left(c_{0a} - \frac{rk_2}{2k_1} \right) \left(1 - e^{-\frac{2k_1}{ru} L} \right) \right]. \tag{21}$$

Case 4. Let $0 < f(c_a) = k_1 c_a$ and $0 < g(c_b) = k_2 c_b$, where k_1 and k_2 are constants.

For this case the solution of equation (8) is identical to that of Case 2. The solution of equation (7), however, is given by the integration and imposition of boundry conditions on the following expression:

$$\frac{dc_a}{dx} = \frac{k_2}{u} c_{0b} e^{-\frac{k_2}{u} x} - \frac{2k_1}{ru} c_a. \tag{22}$$

By performing the above-mentioned operations, we obtain

$$c_a = \left(c_{0a} - \frac{k_2 r}{2k_1 - rk_2} c_{0b} \right) e^{-\frac{2k_1}{ru} x} + \frac{k_2 r}{2k_1 - rk_2} c_{0b} e^{-\frac{k_2}{u} x} . \tag{23}$$

For Case 4 the evaluation of expression (3) is somewhat more complicated than in the first three cases. By substituting the right member of equation (23) into expression (1) and evaluating the integral, we obtain

$$E = 2\pi r e_0 u \left[\frac{r}{2} \left(c_{0a} - \frac{k_2 r}{2k_1 - rk_2} \right) \left(1 - e^{-\frac{2k_1}{ru} L} \right) + \frac{k_1 r c_{0b}}{2k_1 - rk_2} \left(1 - e^{-\frac{k_2}{u} L} \right) \right] . \tag{24}$$

Thus far, expressions have been derived which give E as functions of $f(c_a)$ and $g(c_b)$. Four special cases of the forms of $f(c_a)$ and $g(c_b)$ have been investigated. It remains now to derive an expression for the length of the small intestine of the animal in terms of the animal's mass. In order to simplify the equations, however, we will make the assumption that the digestive process occurs almost entirely at the initial end of the small intestine. In terms of our notation, this assumption can be interpreted to imply that $c_{0b} \cong 0$ and $k_2 \cong 0$.

Using this assumption we can summarize the above cases as follows:

Case 1 and Case 2:

$$c_a = c_{0a} - \frac{2k_1}{ru} x ,$$

$$E = 2\pi k_1 e_0 r L ;$$

Case 3:

$$c_a = c_{0a} e^{-\frac{2k_1}{ru} x} ,$$

$$E = \pi u e_0 r^2 c_{0a} (1 - e^{-\frac{2k_1}{ru} L}) ;$$

Case 4:

$$c_a = c_{0a} e^{-\frac{2k_1}{ru} x} ,$$

$$E = \pi u e_0 r^2 c_{0a} (1 - e^{-\frac{2k_1}{ru} L}) .$$

Since the animals are considered geometrically similar and their volumes considered proportional to their masses, we can write

$$(\text{volume of small intestine}) = \pi r^2 L = \phi M\,, \tag{25}$$

where M denotes the mass of the animal and ϕ is a constant.

Now, by considering the expression for E of Cases 1 and 2, we can solve for L in terms of E. After performing the appropriate algebraic manipulations, we obtain

$$L = \frac{E^2}{4\pi k_1^2 e_0^2 \phi M}. \tag{26}$$

Taking assumption (8) into consideration, equation (26) can be written

$$L = \frac{1}{4\pi}\left(\frac{k}{k_1}\right)^2 \left(\frac{1}{\phi}\right) \frac{1}{e_0^2} M^{2p-1}. \tag{27}$$

The argument for Cases 3 and 4 requires a more definite statement about the relation between c_{0a} and c_{fa} (the initial and final concentrations of A). For this purpose, we will assume that the absorbing system operates at a certain constant level of efficiency

$$\frac{c_{fa}}{c_{0a}} = \lambda\,, \tag{28}$$

λ being some constant fraction. In other words, when $x = L$, $c_a = c_{fa}$. By substituting the above expression into the equations relating c_a with x for Cases 3 and 4, we obtain

$$c_{fa} = c_{0a} e^{-\frac{2k_1}{ru} L}. \tag{30}$$

By solving equation (30) for u and substituting the resulting expression into the expression for E of Cases 3 and 4, we obtain, after some algebraic manipulation, the relation

$$L = -\frac{E}{2\pi c_{0a} k_1 \left(\frac{1-\lambda}{ln\lambda}\right) e_0 r}. \tag{31}$$

Using the same argument as in Cases 1 and 2, we obtain

$$L = \frac{1}{4\pi}\left(\frac{k}{k_1}\right)^2 \frac{1}{\phi}\frac{1}{e_0^2}\left(\frac{ln\lambda}{1-\lambda}\right)^2 \frac{1}{c_{0a}^2} M^{2p-1}. \tag{32}$$

Equations (27) and (32) represent relations between the length of the small intestine, the mass of the animal, and certain factors in the animal's diet. Both equations are consequences of the same general assumptions, differing only by the special case postulates which

were made concerning the forms of the functions f and g. A more thorough analysis would necessitate the investigation of several more special cases using forms of f and g dictated by experiment (e.g., the "loop" technique).

Since several substances of the types A and B are important constituents of the diet of any vertebrate, any relation between L and M would need to take all of the more important substances into consideration if it is expected to approximate reality. In this connection, equation (32) might be given a meaningful interpretation if we were to consider the postulated substance A to be a kind of "average food substance." The constants which pertain to A would then be interpreted to mean the average of those constants associated with all of the A's. In averaging, however, it would of course be necessary to weight each A_i according to its abundance in the animal's diet. This weighting would also be reflected in computing the constants which are to be associated with A. Given such an interpretation, equation (32) could be checked against experimental data. In view of the inadequacy of the analysis, however, we could not expect to obtain better than first order agreement.

It is interesting to note the fashion in which λ, the "efficiency ratio," enters into equation (32). The function $ln^2\lambda/(1-\lambda)^2$ is indefinitely large for $\lambda = 0$. For $\lambda = 1$, the function is of an indeterminate form, but approaches 1 in the limit. The behavior of the function $ln^2\lambda/(1-\lambda)^2$ has the physically plausible implication that in order for the small intestine to absorb all of the available "food," it would need to be indefinitely long, whereas a very short small intestine would leave most of the "food" unabsorbed.

It would be desirable to predict the constant of proportionality between L and M^{2p-1} of equation (32) by measuring its parameters, namely k, k_1, ϕ, λ, c_{0a}, and e_0—the parameters being weighted averages, as mentioned earlier. Values for k could be obtained by standard basal metabolism measurement procedure. The constant k_1 may be evaluated by the use of "loop experiments" (Höber, 1946, pp. 531-552). The measurement of ϕ brings up the problem of giving an exact operational definition for the symbol L. Although most textbooks of comparative anatomy speak of the "length" of the intestine and its components, often giving measurements, no standard measuring procedure is indicated. The need for such a standard method is due to the fact that the length of the intestine varies over a wide range, depending upon the tonus of the muscle tissue and various other physiological factors. Assuming that some such standard measuring procedure, giving comparable values for both the length and volume of the small intestine from animal to animal, could be established, the meas-

urement of ϕ would be straightforward.

The symbol e_0 may be evaluated in the following manner. Consider first the energy changes involved in the over-all metabolism of a typical protein:

$$\text{Protein (solid)} \rightleftarrows \text{Protein (aq)}\,; \qquad \Delta F_{\text{solution of protein}},$$

$$\text{Protein (aq)} \rightleftarrows \sum_{1}^{n} (\text{Amino Acid}_i) + (n-1)\text{H}_2\text{O}\,;$$

$$\Delta F_{\text{hydrolysis}},$$

$$(\text{Amino Acid}_i) \rightleftarrows a^{(i)}\text{CO}_2 + b^{(i)}\text{H}_2\text{O} + c^{(i)}NH_4^+ + d^{(i)}\ \text{urea}\,;$$

$$\Delta F^{(i)}{}_{\text{metabolism}}.$$

The total free energy change is therefore given by:

$$\Delta F = \Delta F_{\text{solution}} + \Delta F_{\text{hydrolysis}} + \Delta F_{\text{metabolism}}\,;$$

hence

$$\Delta F_{\text{metabolism}} = F_{\text{digestion products}} - F_{\text{metabolism products}}.$$

The e_0 of equations (27) and (32) are equivalent to the ΔF of metabolism. The evaluation of e_0, therefore, requires an analysis of the proteins in their diet, their concentration in the intestine, and data concerning the free energy of the digestion products and metabolism products. Some data of the latter are available.

A similar procedure applies also to the evaluation of the e_0 of carbohydrates. By letting $Q = \dfrac{1}{e_0^2} = k\,\dfrac{1}{e_0^2}$, we can write equation (32):

$$L = QM^{2p-1}.$$

It would be interesting now to plot the constant Q for animals having different dietary habits against the e_0 of the various diets. We should expect from equation (32) that

$$\frac{\partial Q}{\partial e_0} = -2ke_0^{-3}.$$

A more thorough analysis would entail a derivation of equations analogous to (27) and (32) without the simplifying assumption that c_{0b} and k_2 are negligible. Such a derivation would also be improved if the general case of n substances of the A type and m substances of the B type, with corresponding forms of f and g, were considered.

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SUGGESTED EXPERIMENTAL PROCEDURE FOR DETERMINING THE SATISFACTION FUNCTION OF ANIMALS

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Some general experimental procedures are suggested to test a previously developed theory of motivation interactions which gives a quantitative description of factors in motivation. The experiments are devised with a view of varying simultaneously the "positive" and "negative" terms of a postulated satisfaction function which is supposed to depend on the subject's "effort" and "remuneration." If the output of effort on the part of the subject reaches a steady state for a given set of conditions, this output is taken to be the optimum output under those conditions. In other words, it is supposed that the satisfaction function is "maximized." From the equations describing the derivatives of the satisfaction function with respect to different variables, the "biological constants" of the individual can be computed and his behavior predicted under a variety of other conditions. In particular, on the basis of previous papers, it should be possible to predict the behavior of two "cooperating" and "sharing" individuals.

I. *Theoretical Considerations*

In developing a mathematical theory of motivation interactions of two individuals, one of the authors (Rapoport, 1947a, 1947b, 1947c, hereinafter referred to as I, II, III) postulated the existence of a "satisfaction function," supposed to determine the motivations for behavior. The function was supposed to consist of two terms. One of them, R, represented the addition to satisfaction resulting from "remuneration," i.e., receiving objects of satisfaction; the other, E, represented detraction from satisfaction resulting from "effort," i.e., the expenditure of energy required to obtain the remuneration. "Optimum effort" was then supposed to maximize the satisfaction function,

$$S = R(r) + E(x), \tag{1}$$

where x was the effort and r the remuneration. The latter was supposed a function of x and, in general, of other variables.

The form of the function R was suggested by Weber's Law. Accordingly, R was taken as a logarithmic function of the remuneration. Some experimental evidence for the form of R appears in the data collected by L. L. Thurstone (1931). On the other hand, the form of E, which was taken as $-\beta x$, i.e., proportional to the effort, has, as far as the authors know, no basis in experimental evidence. It was

arbitrarily selected simply so that a method of constructing a theory could be developed.

The plausibility of a strict logarithmic function for R is, of course, likewise questionable, especially in view of the fact that satisfactions resulting from fulfillments of various needs may exhibit sharp differences. Strictly speaking, it is impossible to measure "satisfaction" directly. But it is possible to infer at least the sign of its derivative with respect to effort for various values of the effort by ascertaining whether the subject tends to increase or to decrease his efforts in a given situation. *By definition* of "satisfaction," increased effort means that for the values of the parameters where the increase of effort is observed, the derivative of the satisfaction with respect to effort is positive.

If it should prove possible to determine the form of the satisfaction function of individual animals, some aspects of the theory of motivation interactions could be tested in experiments involving two animals, who "cooperate" and share the results of their efforts. Certain conclusions from II and III regarding behavior as a function of the sharing formula and of the parameters (especially the cooperation coefficient and the reluctance) could then be tested by experiment.

The satisfaction S of a single individual was taken in previous papers to be a function only of the effort, x, and of the single "biological" parameter β. Hence the optimum output (obtained by setting $\partial S/\partial x = 0$) was a function of the reluctance coefficient β alone. It is clear that this picture, whatever its usefulness for the purpose of developing the method, is too crude to be of any value in an actual experiment. We have no assurance that the satisfaction function resulting from appeasement of hunger is a logarithmic function of the food consumed. All we can reasonably assume is that the motivation for acquiring additional objects of satisfaction decreases as the number of acquired (consumed) objects increases. This postulate implies a decreasing positive first derivative of our satisfaction function with increasing remuneration. L. L. Thurstone (1931) has shown that experimental results fit the logarithmic satisfaction function, which we have also postulated (I, II). But other functions also have this general property. In particular, the function

$$B(1 - e^{-\mu r}), \qquad (\mu > 0), \tag{2}$$

where B and μ are constants, e the base of natural logarithms, and r (a function of x) again the variable remuneration, behaves very much like the logarithmic function. If the function R were measured directly, it would be a moot question whether the difference between the logarithmic function and the function (2) would be outside the

margins of experimental error. In our case, however, the choice between the two functions is significant for the following reasons. In the experiments suggested below, the amount of food available to the subject will be

$$r = k + ax\,, \tag{3}$$

where k is a certain amount independent of effort and a is a parameter representing the efficiency of the subjects' effort. To show the essential difference resulting from the different choices of the form of R, consider for $k = 0$

$$R = A \log r = A \log (ax). \tag{4}$$

Then $\partial R/\partial x = A/x$, independent of a. On the other hand, if we take

$$R = B(1 - e^{-\mu ax}), \tag{5}$$

then $\partial R/\partial x = B\mu a e^{-\mu ax}$, which does depend on a. Now in projected experiments, the efficiency parameter (a) can be varied at will. In the first case the optimum effort $\bar{x}$ will not depend on a, while in the second case it will. Hence we hope to decide which of the two functions (4) or (5) is a closer approximation to the "actual" R. Possibly R is a combination of the two and will be so considered, so that the values of the coefficients A and B will be determined by experiment. We shall therefore take R to be

$$R = A \log (k + ax) + B(1 - e^{-\mu(k+ax)}). \tag{6}$$

Let us now consider $E(x)$. We can generalize our previous assumption, namely, $E(x) = -\beta x$, by taking $E(x) = -\beta(Cx)^{\nu}$. For sufficiently large ν, this means that the detraction from satisfaction is insignificant for small effort and rises sharply at some critical value near $Cx = 1$. The coefficient C will, of course, depend on the units chosen to measure x. We now have our expression for S, namely

$$S = A \log (k + ax) + B(1 - e^{-\mu(k+ax)}) - \beta C^{\nu} x^{\nu}; \tag{7}$$

and for $\partial S/\partial x$,

$$\partial S/\partial x = \frac{Aa}{k + ax} + B\mu a e^{-\mu(k+ax)} - \nu C^{\nu} \beta x^{\nu-1}. \tag{8}$$

Ordinarily, the optimum output $\bar{x}$ would be obtained by setting $\partial S/\partial x = 0$, but we shall obtain it by setting $\partial S/\partial x = \varepsilon$, a threshold value, for reasons which will appear below. When this is done, $\bar{x}$ becomes formally a function of nine parameters

$$\bar{x} = \bar{x}(A, B, C, a, k, \mu, \nu, \beta, \varepsilon). \tag{9}$$

Our problem is to determine those of the parameters which are not fixed in advance. If this can be done, the satisfaction function of an individual animal can be expressed as a function of its effort, and its behavior resulting from motivation interactions with other animals possibly predicted.

Denote $\partial S/\partial x - \varepsilon$ by $G(A, B, C, a, k, \mu, \nu, \beta, \varepsilon, x)$. Then $G = 0$ defines, under suitable restrictions, $\bar{x}$ as a function of the nine parameters. Note that $\bar{x}$ is now the *steady* optimum output. If under certain conditions the work output of an animal reaches a steady state, we shall suppose that it is the optimum output under those conditions. Let us begin by placing the animal into circumstances where $\bar{x} = 0$. This can be done by simply feeding the animal unconditionally. Then $r = k$ and

$$S = A \log (k) + B(1 - e^{-\mu k}). \tag{10}$$

The quantity k is now a measure of food consumed per unit time.* Suppose k reaches a certain "satiation value" $\bar{k}$, which will be the steady amount of food per unit time consumed by the animal with access to an unlimited food supply. Then $\bar{k}$ will be measured directly. We seek to determine μ as a function of other parameters. But note that if S is given by equation (10), $\partial S/\partial k$ never vanishes. Therefore, we shall suppose that motivation to eat more food per unit time* ceases when $\partial S/\partial k$ drops below a threshold value ε. This is the reason for introducing the threshold value in equation (9). Then

$$\partial S/\partial k = A/k + B\mu e^{-\mu k} = \varepsilon \tag{11}$$

determines μ as a function of other parameters. We first set

$$S_k - \varepsilon = A/k + B\mu e^{-\mu k} - \varepsilon = 0\,. \tag{12}$$

We can now solve for B in terms of A, μ, and ε. Substituting this value of B into equation (10) and fixing the value of the *satiation* satisfaction arbitrarily at 100, we have

$$A \log (\bar{k}) + (\varepsilon\bar{k} - A)\, e^{\mu k}/\mu\bar{k} - (\varepsilon\bar{k} - A)\,\mu\bar{k} = 100\,, \tag{13}$$

where $\bar{k}$ is the satiation quantity of food consumed and can be measured directly. Hence μ now becomes a function of A and ε alone.

So far we have "eliminated" (in principle) B and μ. Now the optimum output $\bar{x}$ becomes a function of seven parameters, defined by the equation

$$\bar{x} = \bar{x}(A\,, C\,, a\,, k\,, \nu\,, \beta\,, \varepsilon). \tag{14}$$

Of these, the efficiency coefficient a and the guaranteed subsis-

* The unit of time will be taken large—depending upon the dictates of preliminary experiments—to provide an ample interval for averaging.

tence k can be varied at will and measured directly. In principle, therefore, it is necessary only to give to a and to k five arbitrary pairs of values and to measure the corresponding values of $\bar{x}$ in order to determine the five remaining parameters. In practice, a great many more pairs of values can be given, and the values of $\partial\bar{x}/\partial a$ and $\partial\bar{x}/\partial k$ can be measured directly for different values of a and k.

Let us suppose that the above measurements enable us to determine the parameters. Some of these parameters are "biological," perhaps characteristic of individual animals or of the species. These are μ, ν, β, and ε. Others are "unit parameters." These are A, B (whose determination depends on the choice of units for S), and C (whose determination depends on the choice of units for x). Others are experimental parameters which can be fixed at will. These are a and k. The following procedure is designed to provide further checks on the parameters.

1. Instead of setting the efficiency parameter a constant, make the efficiency a known function of the effort: $a = a(x)$. The substitution of $a(x)$ for a in $G = 0$ transforms this equation into another, from which the new values of $\bar{x}$ can be predicted.

2. It may be possible to vary β by making the work increasingly "unpleasant" for the animal, for example by providing electric shocks whose intensity would increase with an increase of work. It would be necessary to determine just how the animal increases his output of energy when it does increase it—by increasing his speed of working or by increasing the period of working or by some combination of the two. Intensity of shock could be made the function of any of these. Then the reluctance β would have to be taken as $\beta = \beta(\beta_0, V)$ where β_0 is the initial reluctance previously computed and V the voltage used for electric shocks. We would require that $\beta(\beta_0, 0) = \beta_0$ and then empirically determine β as a function of V. This can be done if the values of all the other parameters are known. With such a function determined, we can then set β at will and predict the corresponding changes of $\bar{x}$ for imposed changes of a and k.

3. Further checks on the method would consist of performing the above-mentioned experiments on animals of widely differing masses, ages, and species, on animals of both sexes, noting differences of behavior during the menstrual cycle and during pregnancy in females, and the differences associated with effects of drugs. One could assume various changes in the *biological constants* due to all these factors (the unit constants, of course, remaining the same) and test the validity of the form of the satisfaction function by comparing the observed and predicted changes in $\bar{x}$ associated with changes in a and k.

4. It might be instructive to seek a correlation between the intelligence of individual animals (as determined by their speed of learning in other experiments) and the time it takes them to reach a steady state of output (i.e. to adjust to a new situation in such a way as to maximize the satisfaction function).

5. Finally, the crucial experiments, to which the above-mentioned procedures are intended to lead, would be concerned with the motivation reactions of two or more animals who are made to "cooperate" and "share" according to the equations described in I, II, and III. If the form of the satisfaction function can be determined with any accuracy, then the fact that the sharing formula and the cooperation coefficient can be accurately controlled by the experimenter should enable us to predict the ultimate optimum outputs. It might even be possible to say whether the determination of output will be "symmetric" or "asymmetric"* by watching the adjustment time of the individual animal to new conditions. One of the conclusions implied in II would require that the determination of optimum output would tend to be asymmetric if the adjustment times of the two "cooperating" animals were widely different. The asymmetry should be "in favor" of the animal with the longer adjustment time, and any trend toward parasitism should be observed in that animal (for proper values of the cooperation coefficient).

II. *Experimental Considerations*

The experimental implications to which the foregoing theoretical considerations have alluded are associated with many concepts which have been the subjects of extensive studies by experimental psychologists.

Unfortunately, however, the authors have been unable to find any quantitative data which could be used as a test of the equations. The theory here presented calls for data which relate the "effort" expended by an animal with the "reward" which motivates it. Such data must be obtained for several different experimental conditions.

Quantitative observations have indeed been made on the effects of "reward" in experimental situations. Similar measurements have been made of "effort" expended. In no case, however, have both "reward" and "effort" been measured for a sufficient number of different values in the same experimental setup. The effects of variable "reward" on maze performance have been investigated (Elliott, 1929a, 1929b). It is doubtful, however, whether maze performance can be related in some simple fashion to the "effort" expended in learning.

* For definitions of symmetric and asymmetric determinations of output, see III.

Similarly, the amount of food (reward) eaten by chickens from "hard" or "soft" surfaces has been tabulated (Bayer, 1928). Here again, the "effort" of the fowl cannot readily be related to the reluctance it displays to pecking on a hard surface. Even if such a relation could be established, the number of gradations of hardness which were tested in the experiments is inadequate for a meaningful check of the theory.

The electric grill experiments (Nissen, 1930) cannot be used as a check of the equations for similar reasons. Even if the total "effort" of the animal could be related to the magnitude of the shock it receives from the grill and the number of crossings it makes, the "rewards" (food, water, sex gratification, etc.) are qualitatively different and cannot readily be translated into comparable quantitative terms.

One investigator (Tsai, 1932) made observations on the "efforts" of rats (the animal could make a choice of procedure) while holding the reward constant; he also observed which of several rewards would be chosen if the "effort" required were kept constant. On the basis of these observations he deduced his law of maximum satisfaction and minimum effort: Among several alternatives leading to equivalent satisfactions of some potent organic needs, the animal, within the limits of its discriminative ability, tends to finally select that which involves the least expenditure of energy; among several alternatives involving equivalent expenditures of energy, the animal, within the limits of its discriminative ability, tends to finally select that which leads to the greatest relief of organic needs. However, Tsai failed to investigate the case we are interested in, namely that in which the "reward" is a known increasing function of the "effort" expended.

Experiments discussed above were not devised by the investigators with the express purpose of testing a theory such as the one herein developed. For this reason the data derived are not directly applicable to the equations. The authors therefore propose the following set of experiments to meet this need.

Experiment 1. *Purpose*: To measure the rate $\bar{k}$ (satiation rate) at which the animal will eat if food is always available, that is, if the animal is not required to perform any "task" to obtain it. *Procedure*: In this experiment it will be necessary to measure the steady state. This implies that an interval of time must be chosen such that $\bar{k}$ for any one interval will not vary appreciably from the $\bar{k}$ of successive intervals. Cages used in this and all other experiments are to be of the same dimensions.

Experiment 2. *Purpose*: To measure ($\bar{x}$) as a function of (a). *Procedure*: The animal is placed in a cage which is equipped with a "work-wheel" device. (Several types of "work-wheels" are already standard equipment in laboratories of experimental psychology and physiology). The animal is to be conditioned, by one of the usual procedures, to expect food in an adjacent food trough only when it operates the work-wheel. After conditioning is completed (that is, when the work-wheel procedure is the animal's only source of food) the constant (a) is set. Setting the constant (a) will consist simply of making an adjustment in the apparatus such that the amount of food dispensed by the apparatus will be directly proportional to the number of turns made on the work-wheel, with the constant of proportionality equal to (a). When $\bar{x}$ reaches a steady state, its value is to be recorded with that of (a). In each case, care is to be taken that the steady state has been reached. For each animal whose behavior ($\bar{x}_i$ and a_i) is observed in the sequence a_1, a_2, a_3, $\cdots$, a_n, another animal is to be tested in the reverse sequence, namely, a_n, a_{n-1}, a_{n-2}, $\cdots a_1$.

Experiment 3. *Purpose*: To measure $\bar{x}$ as a function of k. *Procedure*: An animal conditioned as in experiment 2 is to be placed in a cage equipped with a work-wheel. Each day the food trough is to be supplied with a constant amount of food (k) over and above that "earned" by the animal. The values of $\bar{x}$ and k are to be recorded for several values of $k < \bar{k}$. The measurements refer to the steady state.

Experiment 4. *Purpose*: To observe the behavior ($\bar{x}$) of two animals which, unknown to themselves, share the food which they "earn" by operating work-wheels. *Procedure*: Two cages are to have their work-wheel apparatus connected in such a way that the food, which is dispensed according to the work done on one work-wheel, is shared between both food troughs. One animal conditioned as in experiment 2 is to be placed in each of the two cages. Record the $\bar{x}$'s of each of the animals for: (1) a wide range of a's, setting $k = \alpha = 0$, and (2) a wide range of α's, setting $k = 0$, $a =$ constant. (Repeat for different values of $k < \bar{k}$ and a).

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THEORY OF AMEBOID MOVEMENTS

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A theory of the random change of the shape of an ameba, produced by protusion and retraction of pseudopods is developed on the assumption that a local disturbance, which reduces the surface tension, travels along the surface of the ameba. Quantitative relations suggesting experimental verification are derived for the average size and average duration of a pseudopod.

Suppose that in a spheroid cell a local lowering of surface tension occurs which spreads, somewhat like a nerve excitation, with a constant velocity v, and recovers after a while. The local spot of lower surface tension will produce a protrusion, a pseudopod, with the locus of the decreased surface tension at its lobe. Then the decreased surface tension will spread from the lobe towards the base, thus becoming lower, but uniform along the whole pseudopod. The latter will therefore round up. But in the meantime, the original locus of lowered surface tension will have recovered. If everything is perfectly symmetric in the cell, this will result in a flattening of the cell in the direction orthogonal to the axis of the original pseudopod. Then, after the disturbance recovers in the equatorial region and travels to the opposite pole, a pseudopod will be protruded in a direction opposite to that of the original. But due to irregularities both in the internal structure of the cell and in its surface, when the disturbance will have reached the equatorial region, it will not be uniform. There will be a spot of *lowest* surface tension at the equator. This will result in a protrusion of a pseudopod at an angle to the original, rather than in a regular flattening of the cell. Thus instead of regular pulsations of the cell, we shall have irregular changes in shape, resulting in *average* elongations and contractions. As has been shown previously (Buchsbaum, Rashevsky, and Stanton, 1944), such average elongations and contractions may be measured by measuring the ratio P/A of the meridional perimeter P to the area A of the optical cross-section of the cell. This ratio indeed exhibits quasi-periodic changes (*loc. cit.*). If the velocity v of the disturbance is slow and if by the time that it reaches the opposite pole a new disturbance starts, then the average quasi-period T is given by

$$T = \frac{\bar{P}}{v}, \tag{1}$$

where $\bar{P}$ is the average meridional perimeter during the cycle of pulsation. Relation (1) will hold also if we consider that due to the gross asymmetries of the cell, the original disturbance does not spread in all directions, but only in one, traveling around the cell in quasi cycles. This is perhaps biologically even more plausible. Our next problem is to determine $\bar{P}$.

Let us first determine P and A in terms of the constant volume V of the cell and of the ratio $\alpha = r_1/r_2$ of length to width. For a *cylindroid* cell we have

$$P = 4(r_1 + r_2); \quad A = 4r_1r_2; \quad V = \frac{4}{3}\pi r_1/r_2^2. \tag{2}$$

Putting

$$a^3 = \frac{3V}{4\pi}, \tag{3}$$

we have

$$r_1r_2^2 = a^3. \tag{4}$$

Equation (4), together with $r_1/r_2 = \alpha$ gives

$$r_1 = a\,\alpha^{2/3}; \quad r_2 = a\,\alpha^{-1/3}. \tag{5}$$

Hence from equation (2)

$$P = 4a(\alpha^{2/3} + \alpha^{-2/3}); \quad A = 4a^2\,\alpha^{1/3}; \quad P/A = a^{-1}(\alpha^{1/3} + \alpha^{-1}). \tag{6}$$

Now let us consider the *average* variation of r_1 under the effect of a local decrease of surface tension at one of the poles. To this end we may consider a cell of length r_1 and width r_2, which has a surface tension γ on the "sides" and on *one* of the "ends," but has a lower surface tension $\gamma_1 < \gamma$ at the other "end." We shall neglect here the effect of the volume forces due to diffusion, and study only the effect of the surface tension.

Applying Betti's theorem, just as in the case of cell division (Rashevsky, 1940, chap. iii), we have again, with the same notations,

$$\frac{1}{r_1}\frac{dr_1}{dt} = \frac{1}{3\eta V}\int_s [zZ_\nu - \tfrac{1}{2}(xX_\nu + yY_\nu)]\,dS. \tag{7}$$

On the "sides" we have again

$$\tfrac{1}{2}\int_s (xX_\nu + yY_\nu)\,dS = -\gamma\, r_2\left(\frac{1}{r_1} + \frac{1}{r_2}\right) \times 2\pi r_1r_2, \tag{8}$$

whereas this expression is zero at the "ends."

At the "ends" we have now

$$\int_s zZ_v\, dS = -\pi r_2^2 \left(\gamma_1 r_1 \frac{2}{r_2} + \gamma r_1 \frac{2}{r_2} \right). \tag{9}$$

Equation (7) now becomes

$$\frac{1}{r_1}\frac{dr_1}{dt} = \frac{1}{2\eta}\,\frac{\gamma r_2 - \gamma_1 r_1}{r_1 r_2}, \tag{10}$$

or

$$\frac{dr_1}{dt} = \frac{\gamma - \gamma_1 \alpha}{2\eta}. \tag{11}$$

Since what we actually measure in an irregularly shaped cell is not r_1 but the ratio $\alpha = r_1/r_2$, which is obtained from the last relation (6), therefore we shall introduce α as the unknown variable in equation (11). We find, because of the first equation (5),

$$\frac{d\alpha}{dt} = \frac{3\alpha^{1/3}}{2a}\,\frac{\gamma - \gamma_1\alpha}{2\eta}. \tag{12}$$

If $\gamma > \gamma_1\alpha$, the cell elongates in the direction r_1, forming a pseudopod. But $d\alpha/dt = 0$ when

$$\alpha = \gamma/\gamma_1, \tag{13}$$

which is the maximum length of elongation in this case.

From here on we may use two procedures.

A. We consider as a very rough approximation, that the average value of α is equal to

$$\bar{\alpha} = \tfrac{1}{2}\frac{\gamma}{\gamma_1}. \tag{14}$$

Then the first of equations (6) gives:

$$\bar{P} = 4a(\bar{\alpha}^{2/3} + \bar{\alpha}^{-2/3}) = 4a[(\gamma/2\gamma_1)^{2/3} + (\gamma/2\gamma_1)^{-2/3}]; \tag{15}$$

$$\bar{A} = 4a^2\,\bar{\alpha}^{1/3} = 4a^2(\gamma/2\gamma_1)^{1/3}; \tag{16}$$

$$\frac{\bar{P}}{\bar{A}} = a^{-1}\,[(\gamma/2\gamma_1)^{1/3} + (\gamma/2\gamma_1)^{-1}]. \tag{17}$$

Equation (1) now gives

$$T = \frac{4[(\gamma/2\gamma_1)^{2/3} + (\gamma/2\gamma_1)^{-2/3}]}{v}\,a. \tag{18}$$

The quantity $\bar{P}/\bar{A}$ is directly measurable using a previously discussed method (Buchsbaum, Rashevsky, and Stanton, 1944); so also is the quantity T. Because of equation (13), we have

$$T \propto V^{1/3}; \qquad \bar{P}/\bar{A} \propto V^{-1/3}. \tag{19}$$

The first of those expressions is at least qualitatively in agreement with observations of *Amoeba Chaos chaos* and *Limax*.

We may consider that the right side of expression (12) has a constant average value, obtained by introducing into it the value $\bar{\alpha} = \gamma/2\gamma_1$. This gives

$$\frac{d\alpha}{dt} = \frac{3\gamma(\gamma/2\gamma_1)^{1/3}}{8\eta a} = \frac{K}{a}, \tag{20}$$

with

$$K = \frac{3\gamma(\gamma/2\gamma_1)^{1/3}}{8\eta}. \tag{21}$$

From equation (20) we have

$$\alpha = \frac{K}{a}t + K_1, \tag{22}$$

where K_1 is an integration constant. If we choose the origin of time so that at $t = 0$ the cell is rounded up and has no pronounced pseudopods, then $K_1 = 1$, and we have

$$\alpha = \frac{K}{a}t + 1. \tag{23}$$

The maximum elongation will roughly occur for $t = \frac{1}{2}T$, at which moment it will be equal to $\alpha_{max} = \frac{K}{2a}T + 1$. Hence the average $\bar{\alpha}$ is given very roughly by

$$\bar{\alpha} = \frac{K}{4a}T + 1. \tag{24}$$

This, of course, holds only if the velocity v is large enough, so that T is smaller than the time during which a pseudopod reaches its maximum length.

Introducing equation (24) into the first equation (6), and the latter into equation (1), we find

$$T = \frac{4a}{v}\left[\left(\frac{K}{4a}T + 1\right)^{2/3} + \left(\frac{K}{4a}T + 1\right)^{-2/3}\right]. \tag{25}$$

If this equation is resolved with respect to T, we obtain T as a function of a (hence, of V) and of the other parameters. Introducing that value of T into equation (24), and then the latter into equations (6), we shall determine $\bar{P}/\bar{A}$ as a function of V. Unfortunately, equation (25) cannot be solved in closed form.

Observations show, however, that α may be as high as 3 or 4. In that case, as a very rough approximation, we may omit 1 in equation (23) and omit $\alpha^{-2/3}$ in the first equation (6). Then equation (25) simplifies and leads again to relations (19).

In verifying relations (19) experimentally, we should keep in mind that the ratio P/A discussed here is the *true* ratio for the cell. When the apparent size of a cell is magnified n times by a microscope, the ratio P_a/A_a in the magnified picture is equal to

$$P_a/A_a = \frac{1}{n}(P/A). \tag{26}$$

Since the second relation (19) shows that the true $\bar{P}/\bar{A}$ varies inversely as the true linear dimension, it is readily seen that the apparent P_a/A_a will vary inversely as the apparent size of $l_a = nl$. For we have for two cells, which we distinguish by the indices 1 and 2,

$$\frac{(\bar{P}/\bar{A})_1}{(P/A)_2} = \frac{l_2}{l_1}. \tag{27}$$

Hence, because of equation (26),

$$\frac{(\bar{P}_a/\bar{A}_a)_1}{(\bar{P}_a/\bar{A}_a)_2} = \frac{\frac{1}{n}(\bar{P}/\bar{A})_1}{\frac{1}{n}(P/A)_2} = \frac{l_2}{l_1} = \frac{l_{a2}}{l_{a1}}. \tag{28}$$

The treatment in this paper may be generalized in the following way. Let the radius r_p of the region of reduced surface tension γ_1 be much smaller than either r_1 or r_2. We may then consider the following situation. Let us have a spheroid cell, with $r_1 \cong r_2$. Let the surface tension be equal to γ on the "sides," on one "end," and in the annular region with radii r_2 and $r_p < r_2$ on the other side. The remaining surface of area πr_p^2 is characterized by a surface tension $\gamma_1 < \gamma$. Equation (8) remains unchanged, but instead of equation (9) we now have

$$\int_s zZ_v dS = -\pi r_2^2 \gamma\, r_1 \frac{2}{r_2} - \pi(r_2^2 - r_p^2)\gamma\, r_1 \frac{2}{r_2} - \pi r_p^2 \gamma_1 r_1 \frac{2}{r_2}. \tag{29}$$

Therefore, equation (7) now gives

$$\frac{1}{r_1}\frac{dr_1}{dt} = -\frac{\gamma}{2\eta}\frac{r_1 - r_2}{r_1 r_2} + \frac{2\pi r_1 r_p^2}{3\eta V r_2}(\gamma - \gamma_1). \tag{30}$$

For $r_1 = r_2$, $dr_1/dt > 0$. If $r_p << r_2$, we can consider approximately that the average rate of elongation of the cell, given by equation (28), actually represents the rate of growth of the pseudopod of radius r_p. Setting the right side of equation (30) equal to zero, we find the maximum length of the pseudopod, as well as its duration.

Equation (30) suggests a different approach to the problem of ameboid movements, which may lead to more general results. Assume that "spots" of low surface tension occur at random on the surface of a cell. Then their sizes and durations will follow the normal distribution curve, or some other similar distribution function. Each "spot" will give rise to a pseudopod, whose length and duration is determined by equation (30) and by the duration of the "spot." In that way, we may find an expression for the distribution of the sizes, durations, and numbers of pseudopods in an ameba, and those expressions may be verified experimentally.

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BOOK REVIEWS

RUDOLF K. LUNEBURG. *Mathematical Analysis of Binocular Vision.* 1947. vi + 104 pp. Princeton: Princeton University Press. (Published for the Dartmouth Eye Institute.) $2.50.

This book develops a psychometric of the space of binocular vision. In elegance of derivation and simplicity of result it could hardly be surpassed. To whatever degree the psychometric here presented may appear to be an oversimplification—as any conceptualization must be—this is an achievement, and future developments of the problem here undertaken are almost certain to be measured with reference to it.

The author introduces his development with several expository chapters. There he describes the nature of a psychometric in general and defines the metric in terms of degree of contrast. He explains in elementary terms the nature of a Riemannian metric and the possibility of distinguishing a Euclidean from a non-Euclidean manifold by means of measurement intrinsic to the manifold. Geodesics and Levi-Civita's parallelism are described for subsequent use, and concurrently with these developments the author introduces angular coordinates in terms of which he will ultimately represent his metric.

Of these angular coordinates, two systems are fundamental. The system r, ϕ, θ is referred to the two eyes, representing the angle of convergence, the deviation from the medial plane as measured at the Cyclopean eye (placed on the Vieth-Muller circle), and the angle of elevation. The interocular distance enters as an essential parameter. The system r^*, ϕ^*, θ^* is similar except that it is referred to a fixed base line along the shoulder, the head being allowed to rotate about a vertical axis. The distance of the interocular line from this axis of rotation enters here as a second essential parameter.

The key to the development now lies in the following suppositions. Spatial judgments made with fixed head are in general different from those made with moving head; either is expressible in terms of a distance element ds formed from the unstarred or the starred coordinates as the case may be; but the quadratic form ds^2 describing the one case is the same form in the unstarred coordinates as the corresponding form in the starred coordinates which describes the other case. In other words, let the subscripted variables u_i designate the r, ϕ, θ, respectively, and u_i^* designate r^*, ϕ^*, θ^*. Then if

$$ds^2 = \Sigma\, g_{ij}(u)\, du_i\, du_j$$

represents the "fixed-head" metric, the assumption is that

$$ds^2 = \Sigma\, g_{ij}(u^*)\, du_i^*\, du_j^*$$

represents the "moving-head" metric, where each function g_{ij} in the second form is identical (and *not* the tensorial transform) with the function g_{ij} in the first form.

This assumption is, of course, subject to empirical test, at least in principle. In the present development it is introduced as a plausible assumption only, as an

aid in the argument, and receives indirect confirmation with that of the resulting metric. The author phrases his subsequent deductions in terms of either the starred or the unstarred system, according to convenience, results in one case being immediately applicable to the other.

If a 6-parameter family of rigid translations are to exist the space must be one of constant curvature—elliptic, hyperbolic, or Euclidean. Requirements of symmetry further delimit the character of the functions g_{ij}. Next it is supposed that if two line elements drawn from the same sagittal axis have the same differentials dr and $d\phi$, they will appear to include equal angles with this sagittal axis. The outcome now is

$$ds^2 = M^2(r)\,(\sigma^2\,dr^2 + d\phi^2 \cos^2\phi\,d\theta^2)$$

where σ is a constant, and $M(r)$ has either of the three forms sech $\sigma(r + \mu)$, $2\exp[-\sigma(r + \mu)]$, or csch $\sigma(r + \mu)$, according to whether the space is elliptic, Euclidean, or hyperbolic. Preliminary preference is assigned to the third possibility as the only one for which the ratio of apparent to physical size does not approach zero as the object is moved towards infinity.

The argument outlined so far constitutes almost exactly one half of the book. The remaining part is taken up with applications providing qualitative and quantitative support for the conclusions, and leading toward an evaluation of the parameters σ and μ. Some of the experimental data are taken from current and hitherto unpublished work at the Dartmouth Eye Institute.

The Vieth-Muller circles take on some importance, not as horopters, but as loci $r =$ const. The first set of observations deals with a pair of pencils of rays intersecting on one of these circles, and which, properly observed, appear to lie on a certain cone through this circle. Next the horopter curves are identified with the geodesics in the metric and their equations determined in each of the three geometrics. The "alley" problem—construction of lines parallel to the sagittal axis—is found to contain an ambiguity: the lines may be made geodesically equidistant from the axis, or they may be interpreted in terms of angle. A discordance among findings of different investigators is thereby resolved.

Most interesting is the final chapter developing the 6-parameter group of "rigid translations" in the hyperbolic space of binocular vision utilizing the results of the Dartmouth investigations. In non-mathematical language the problem has to do with the existence of congruent configurations in varying locations. In a space of constant curvature, such as a Euclidean space or a spherical space, it is possible to move a configuration about in the space without changing its shape. In spaces of varying curvature it may be that any motion whatever will of necessity distort the shape. One must understand, of course, that a "rigid" translation in the hyperbolic visual space is *not* a rigid translation in the objective space, nor vice versa. Objects separated in space and psychometrically congruent will in general differ in their physical measurements. Hence one can construct a multitude of figures that are psychometrically (i.e., subjectively) congruent to a given, objectively rectangular, figure, while they themselves are objectively non-rectangular.

What implications the theory may provide for the guidance of designers of binocular instruments, the author does not here develop. Unquestionably the Dartmouth group will not be slow in ferreting them out. One of the most curious effects of instrumented vision is the "induced size effect" uncovered by the Dartmouth investigators some years ago. This effect seems to be due specifically to the disparity of the angles at the two eyes, whereas Luneburg develops his theory

to apply only in the absence of such disparity. It will be interesting to see how natural an extension can be made.

It should be noted carefully that the metric has the property that small angular differences acquire increasing subjective weighting, through the presence of the factor $\operatorname{csch}^2 \sigma(r + \mu)$ in the form ds^2, as the angle of convergence decreases. It has been suggested (e.g., by Householder and Landahl, *Mathematical Biophysics of the Central Nervous System*) that judgments of local deviation from the point of fixation are probably based upon retinal disparities and hence differ intrinsically from judgments of gross distance from the subject which are probably based upon binocular convergence, aerial perspective, etc. Luneburg's psychometric is clearly consistent with this suggestion.

The author scrupulously refrains from any discussion of physiological mechanisms and this is one of the merits of the presentation. But a reviewer may, perhaps, be permitted to indulge in some reflection on a point that is relevant to the applications but not to the validity of the theory. No mention is made of the position of the eyes at any time, nor to the possible presence or absence of fusion. Clearly, however, the development of a binocular space can be effected only after the association of points on one retina with points on the other in a one-to-one fashion, any pair of associated points appearing as images of one and the same external point. These may, in fact, be images of the same point, as in normal vision, or they may not, as in the case of the pencils intersecting on the Vieth-Muller circles. In any case the theory presupposes the association made by some means, but is silent as to the mechanics of the association or whether association of nonfused images is possible. But what of cases of anomalous fusion, such as those reported by Brock in the optometric journals? Do these, if real, bring about a distortion of the metric?

These final remarks and questions imply no criticism of the Luneburg metric. Quite the contrary, they, and a host of others raised by a reading of the text, are indicative of the fruitfulness of the approach. The Luneburg metric, in this reviewer's opinion, represents an extremely significant contribution to the theory of binocular vision.

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